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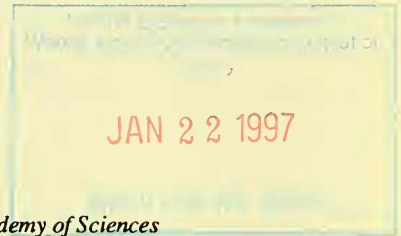
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DESCRIPTION OF FOUR NEW SPECIES OF PHANEROBRANCH
DORIDS (MOLLUSCA: NUDIBRANCHIA) FROM THE
INDO-PACIFIC, WITH A REDESCRIPTION OF
GYMNODORIS AURITA (GOULD, 1852)

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Four species of phanerobranch dorid nudibranchs are described. *Nembrotha mullineri* is known only from the Philippine Islands; *Nembrotha milleri* is known from the Philippines and Indonesia. *Nembrotha chamberlaini* has a somewhat wider distribution and is a member of the *Nembrotha lineolata* complex. *Notodoris serенаe* occurs from Indonesia to Belau and north to Okinawa and differs externally and internally from its congeners, all of which have a yellow rather than gray body color. *Gymnodoris aurita* (Gould, 1852) is redescribed from specimens collected from the Philippines.

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The tropical Indo-Pacific is rich in its diversity of opisthobranch gastropods (Gosliner, 1993; Ghiselin, 1993; Gosliner and Draheim, 1996). The western Pacific is especially diverse in its opisthobranch fauna. Recent collections from several western Pacific localities, including Papua New Guinea, Indonesia, the Philippines and Okinawa have yielded specimens of several large, conspicuous phanerobranch nudibranchs. This paper redescribes one species, not recorded in the literature since its original description in 1852, and describes three species of *Nembrotha* and one of *Notodoris*.

SPECIES DESCRIPTIONS

Family GYMNODORIDIDAE Odhner, 1941

Gymnodoris Simpson, 1855

Gymnodoris aurita (Gould, 1852)
(Figs. 1A, 2A-D, 3A-D)

Doris aurita Gould, 1852:299, pl. 23, figs. 394, 394a.
Gymnodoris sp. Gosliner, Behrens and Williams,
1996:172, fig. 607.

MATERIAL EXAMINED. — Neotype: CASIZ 096243, one specimen, 2 m depth, near Bonito Island Resort, Culebra Island, Batangas Province, off Luzon, Philippines, 18 March 1994, R. Jackson. CASIZ 103751, two specimens, one dissected, 7 m depth, Sabang, Mindoro, Philippines, 1 March 1995, T. M. Gosliner and G. C. Williams. CASIZ 105636, one specimen, 1 m depth, Cemetary Beach, Maricaban Island, Batangas Province, Luzon, Philippines, 19 February 1995, R. McPeak. CASIZ 106524, one specimen, 10 m depth, Layaglayag, Maricaban Island, Batangas Province, Luzon, Philippines, 19 April 1996, M. D. Miller.

DISTRIBUTION. — This species, described from Fiji (Gould, 1852), is also known from the Batangas Province, Philippines and from photos by Roger Steene from Rinca Island, Indonesia (present study).

NATURAL HISTORY. — This species has been observed feeding upon tritoniid nudibranchs of the genus *Marionia* (Mark Prein, pers. comm.). It inhabits shallow water reefs and is active nocturnally.

EXTERNAL MORPHOLOGY. — The body is firm and limaciform. The mantle is reduced and indistinct. The preserved specimens are up to 70 mm in length. The living animals (Fig. 1A, 2A), measure over 100 mm and are orange to deep red with large white to yellowish white tubercles dispersed uniformly over the body. The tubercles are situated on a series of longitudinal wrinkles and folds in the notal surface. The margin of the foot also has a yellowish white band as do the bases of the auriculate oral tentacles. The eight multipinnate gills are large, twice the animal's width, translucent white to red, with white to yellowish white ridges. The rhinophores are white to yellow, short and perfoliate, with 15 steeply set lamellae. They appear to attach to the body more at an angle rather than being strictly perpendicular to the axis of the rhinophore.

The body wall is thick and muscular. There is a network of numerous, densely set subcutaneous glandular tubes, presumably having a defensive function (Fig. 2B). They occur much more densely anteriorly to the gills than posteriorly.

The genital aperture is located anteriorly, just posterior to and at the level of the rhinophores.

BUCCAL ARMATURE. — The buccal mass is thick and muscular. At its posterior end are massive salivary glands (Fig. 2C), measuring over one half the length of the body. The labial cuticle is reduced to a thin chitinous membrane. The radular formula in one specimen is $27 \times 37.0.37$. All the radular teeth lack denticles. The inner lateral tooth (Fig. 3A) is broad and thick, with a wide triangular cusp. The succeeding laterals (Fig. 3B-D) are markedly different from the inner lateral and have a thin, elongate cusp. They become increasingly elongate towards the outer margin.

REPRODUCTIVE SYSTEM. — As in other members of the genus, the gonad is separated from the digestive system. The reproductive system is tri-aulic (Fig. 2D). The preampullary duct is short and narrow. It expands into a wide saccate ampulla, which divides into the short oviduct and elongate vas deferens. The oviduct has a bulbous dilation that may function as a fertilization chamber. From this point the oviduct enters the massive female gland mass via a short duct and branches to an elongate uterine duct. It joins the saccate receptaculum seminis via a short, curved duct, and continues proximally until it widens slightly and enters the massive, thin-walled bursa copulatrix. The elongate, wide vagina also emerges from the base of the bursa and joins the vas deferens near the genital aperture. The vas deferens widens into a huge, curved prostatic portion which has a series of longitudinal glandular ridges along its surface. The vas deferens again narrows into an elongate, curved ejaculatory segment that is muscularized. Towards the distal end of this muscular portion are a series of rows of curved, chitinous spines (Fig. 2E).

DISCUSSION. — Most species of *Gymnodoris* are white or yellowish in general body color. Only a few species are orange or reddish, including *Gymnodoris inornata* (Bergh, 1880) (Gosliner, 1987, fig. 187) and *Gymnodoris* sp. (Wells and Bryce, 1993, fig. 99, as *G. aurita*). The only described, large reddish species with

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FIGURE 1. Living animals. A. *Gymnodoris aurita* (Gould, 1852), specimen from Rinca Island, Indonesia, photo by Roger Steene. B., C. *Nembrotha chamberlaini* sp. nov. specimens from Batangas, Luzon, Philippines, photos by Marc Chamberlain.



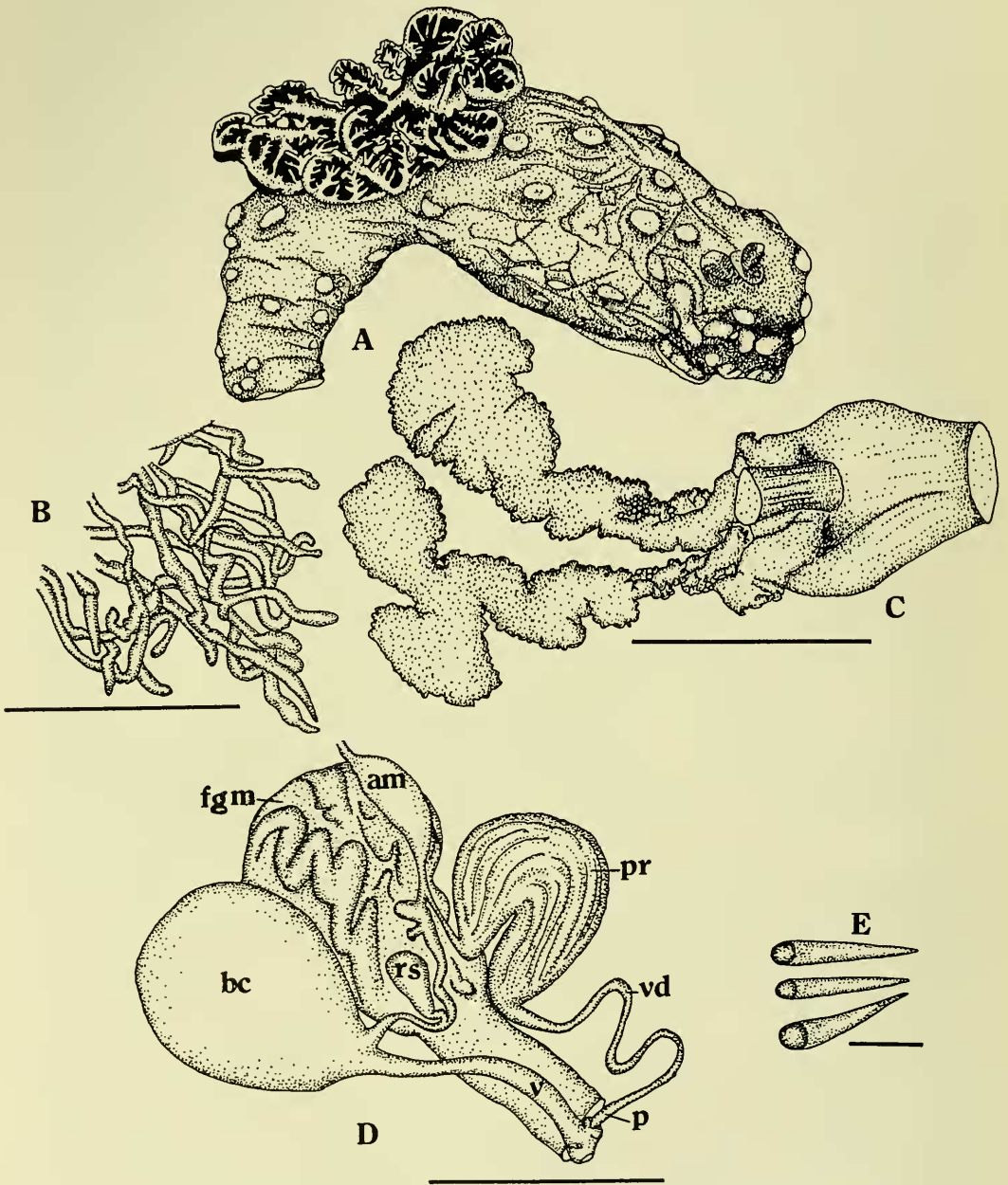


FIGURE 2. *Gymnodoris aurita* (Gould, 1852). A. Living animal. B. Subcutaneous glandular network, scale = 10 mm. C. Buccal bulb and salivary glands, scale = 10 mm. D. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 10 mm. E. Penial armature, scale = 0.05 mm.

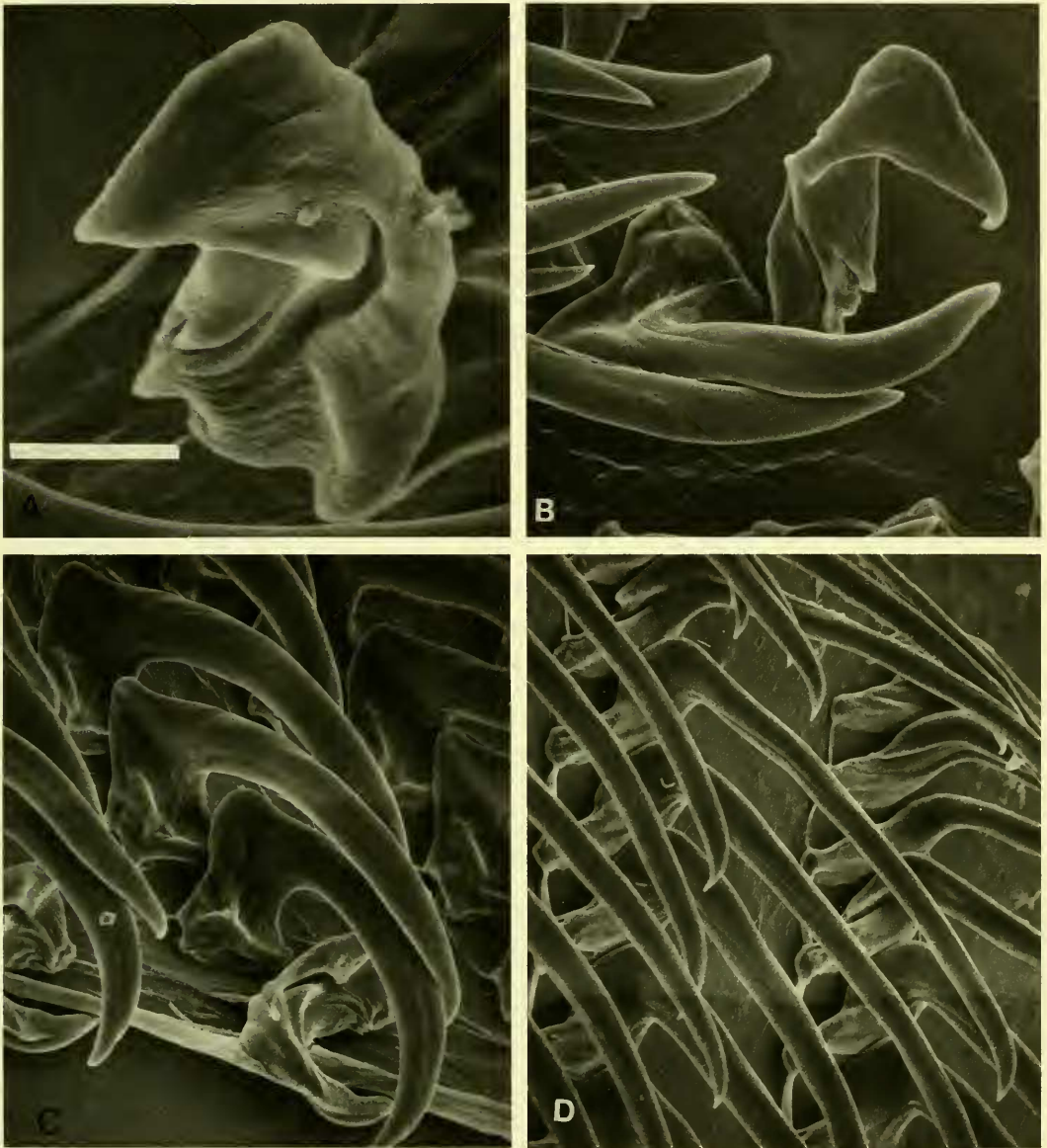


FIGURE 3. *Gymnodoris aurita* (Gould, 1852). Scanning electron micrographs of radula. A. Right inner lateral tooth, scale = 25 μm . B. Left inner lateral tooth, scale = 60 μm . C. Medial lateral teeth, scale = 75 μm . D. Outer lateral teeth, scale = 75 μm .

prominent tubercles is *Gymnodoris aurita* (Gould, 1852). The present material closely matches the original color plates depicted by Gould (1856), and there is little question that they represent the same species. No description of internal anatomy was presented in the original or

subsequent descriptions. No type specimen is extant. All of the nudibranch types from the United States Exploring Expedition have been lost, if indeed they were ever preserved (Johnson, 1964:32). Owing to the absence of type material,

a neotype of *Doris aurita* is here designated, as this represents the first revision of the taxon.

Another large tuberculate, reddish species was illustrated from Australia and identified by Wells and Bryce (1993, fig. 98) as *G. aurita*. This species is likely undescribed and differs in having dark maroon rhinophores and gills while those of *G. aurita* are the same whitish yellow color as the body tubercles. It also has larger, more densely distributed tubercles than does *G. aurita*. Also, *G. aurita* has a wide yellow margin to the foot that is absent in *Gymnodoris* sp. The internal anatomy of *Gymnodoris* sp. is unknown. Nevertheless, the two species are clearly distinct in their external anatomy and coloration.

Family POLYCERATIDAE Alder and
Hancock, 1845

Nembrotha Bergh, 1877

Nembrotha chamberlaini sp. nov.
(Figs. 1B, C; 4A, B; 5; 6A-D)

Nembrotha sp. Okutani, 1994:222; Colin and Arneson, 1995:188, fig. 890; Gosliner, Behrens and Williams, 1996:170, fig. 602.

TYPE MATERIAL. — Holotype: CASIZ 107227, 10-25 m, Kirby's Rock, Maricaban Island, off Batangas, Luzon, Philippines, 18 February 1992, T. M. Gosliner. Paratypes: CASIZ 083689, two specimens, one dissected, same locality, date and collector as holotype.

ETYMOLOGY. — *Nembrotha chamberlaini* is named for Dr. Marc Chamberlain of San Diego, California, a friend, underwater photographer and opisthobranch enthusiast, who has contributed much to our understanding of Pacific biodiversity and has supported publication of these works.

DISTRIBUTION. — Thus far this species is known only from the Luzon and Mindoro Islands in the Philippines (present study) and Okinawa (Okutani, 1994).

NATURAL HISTORY. — *Nembrotha chamberlaini* is a predator upon the tunicates *Rhopalaea* sp., *Clavellina moluccensis* (Sluiter, 1904) and *Oxycorynia fascicularis* Drasche, 1882 (Gosliner, Behrens and Williams, 1996; present study).

EXTERNAL MORPHOLOGY. — The body is elongate and limaciform reaching, up to 62 mm in length, in preserved animals and 100 mm in living ones. The color is complex and variable. The living animals (Fig. 1B, C; 4A) are white with a dark brown to black saddle. The dorsal surface of the head and rhinophores is uniformly bright red, as are the gills, their bases and the posterodorsal portion of the foot. The entire body surface is textured with a pattern of longitudinal wrinkles. The wrinkles are more noticeable on lightly colored surfaces. The margin of the foot is delineated by a blue to purple band, within which a yellow band is present. The foot corners and cephalic ridge are also bluish purple. The anteriormost edge of the notum below the rhinophores is dark brown to black. Ventral to the limit of the red and dark brown pigment is a thin line of yellow, which traces the irregular edges of the red and brown patches. Ventral to the yellow line is an area of opaque white, which may be small or may occupy most of the lateral surface of the animal (Fig. 5). There are two, variably sized, translucent spots posterior to the rhinophores, through which the dermal eyes are visible. These patches may vary from tear drop-shaped to attached rhomboids. These patches are outlined in yellow. The genital apertures, when extended, form a trumpet-shaped structure that is blue to purple. The rhinophores are perfoliate bearing 41–46 lamellae. The five gills are tripinnate. The body wall is highly muscular. The genital aperture is located midway between the gills and rhinophores.

BUCCAL ARMATURE. — There is a large, well-developed blood gland, which is granular in texture and which inserts into the dorsal surface of the esophagus. The buccal mass is relatively elongate and tubular. The salivary glands are short and thick. The labial cuticle is well-developed and chitinous, but devoid of thickenings or denticles. The radular formula is $32 \times 8.1.1.1.8$ (Fig. 6A) in the single specimen examined. The broad rachidian teeth are asymmetrical with two elongate denticles on the left side and three on the right (Fig. 6B). The two inner denticles of the right half of the rachidian may represent a single bifurcate denticle that are united only at the base. The innermost lateral is a large, hamate hook, with a large basal triangular cusp and a similarly shaped primary cusp. No other denticles are present. The outer laterals are rectangular

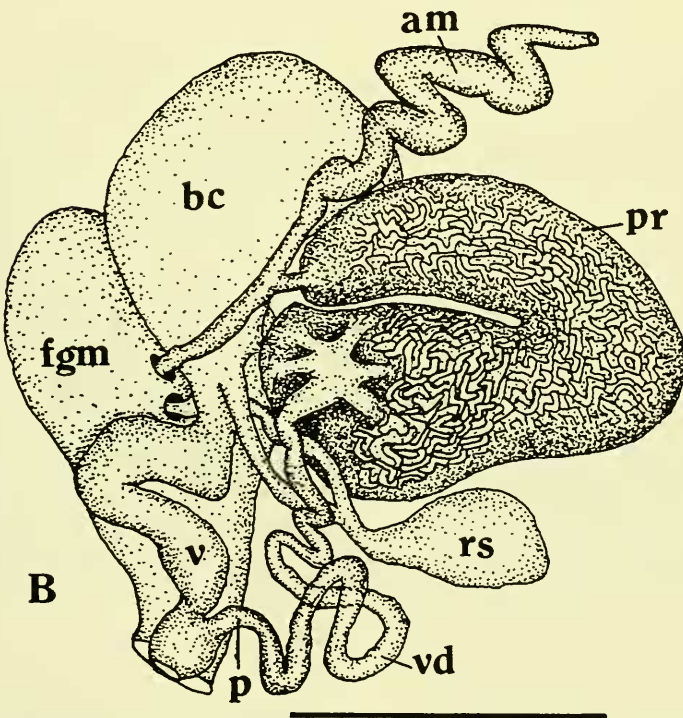
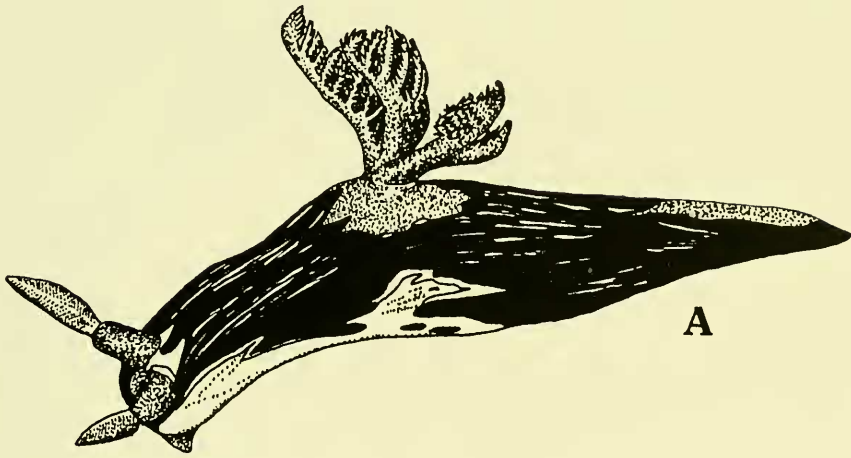


FIGURE 4. *Nembrotha chamberlaini* sp. nov. A. Living animal. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 10 mm.

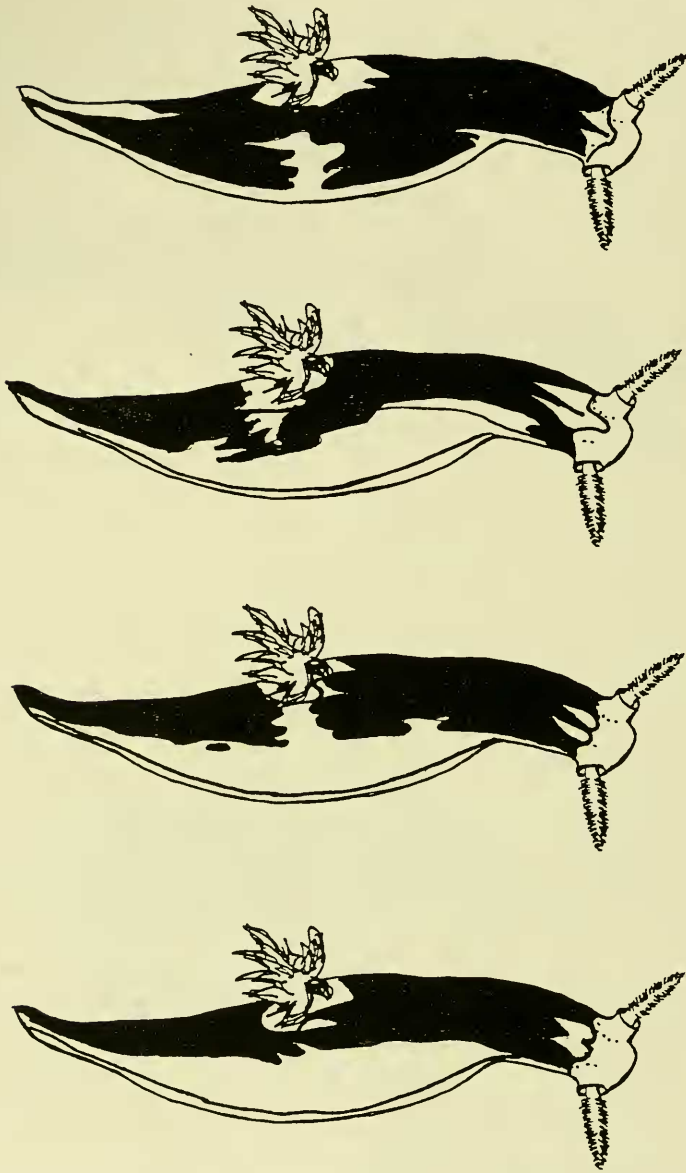


FIGURE 5. *Nembrotha chamberlaini* sp. nov. Variation in distribution of color pattern.

plates, which lack cusps or dentition and become smaller near the margin.

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Fig. 4B). The preampullary duct is short and narrow. It expands into a narrow highly convoluted ampulla which divides into an elongate oviduct and the vas deferens. From this point the oviduct enters the massive female gland

mass. The short branch of the vas deferens widens into a huge, curved prostatic portion which has a dense network of interconnecting tubules over its surface. The vas deferens again narrows into an elongate, highly convoluted ejaculatory segment that is muscularized. Within the distal end of this muscular portion are a series of 14 rows of curved, chitinous hooks which evert into

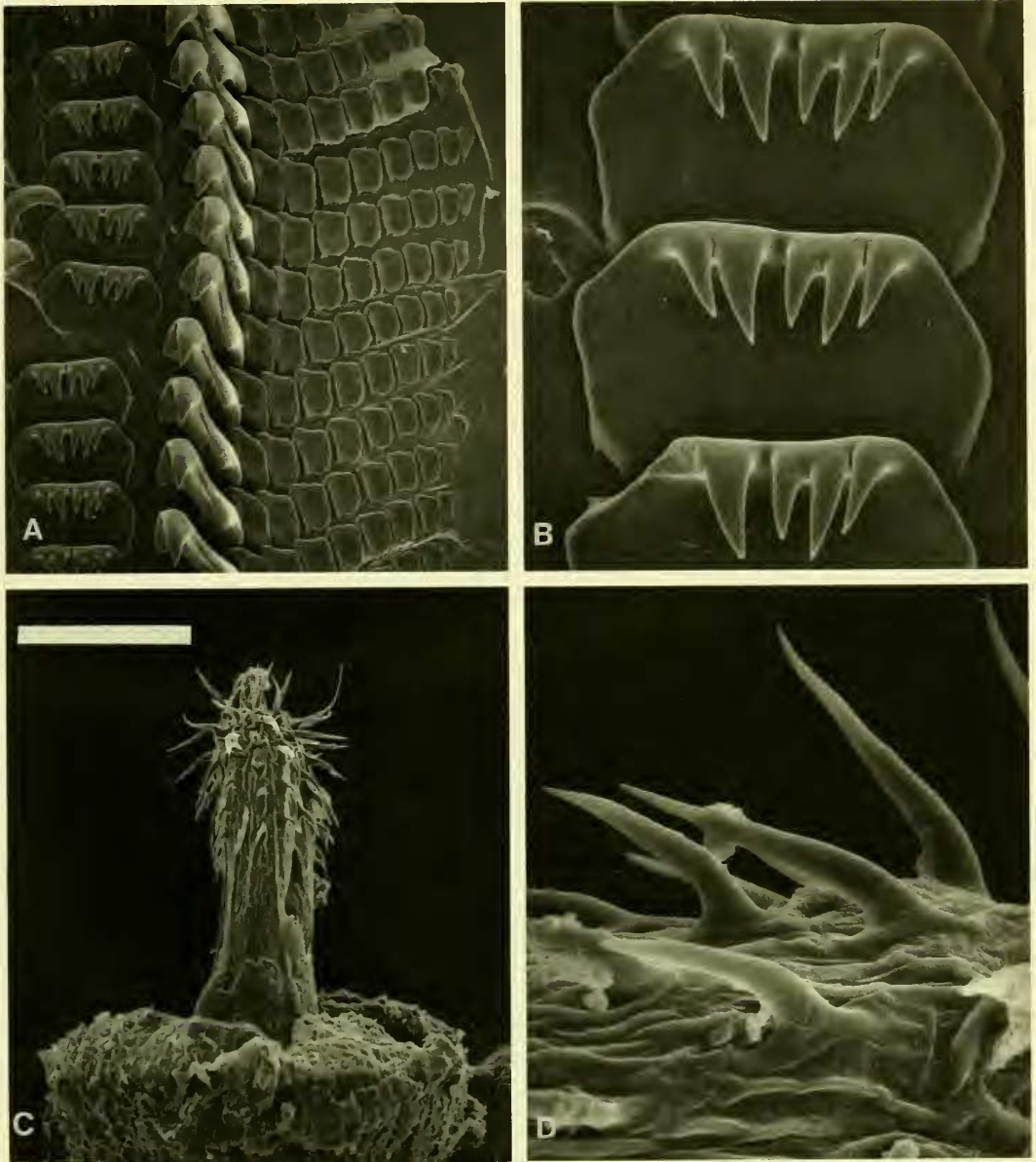


FIGURE 6. *Nembrotha chamberlaini* sp. nov. Scanning electron micrographs. A. Half-row of radular teeth, scale = 250 μ m. B. Rachidian teeth, scale = 75 μ m. C. Protruded penis, scale = 150 μ m. D. Penial armature, scale = 25 μ m.

a penial papilla (Fig. 6C, D). The elongate uterine duct emerges from the female gland mass and joins the saccate receptaculum seminis via a curved duct, and continues proximally until it widens slightly and enters the massive, thin-walled bursa copulatrix. In situ, the bursa is entirely surrounded by the prostate. In Fig. 4B,

the prostate has been teased apart from the prostate and is shown positioned to the side. The elongate, wide vagina also emerges from the base of the bursa and joins the vas deferens near the genital aperture.

DISCUSSION.— This species with its broad, simply denticulate rachidian, is clearly placed in

Nembrotha, as characterized by Burn (1967) and Cervera, García-Gómez and Megina (1996). Cervera, García-Gómez and Megina compared the four described species of *Nembrotha* that have whitish bodies with darker markings on the dorsal and lateral surface: *N. lineolata* Bergh, 1905 (Coleman, 1989:10; Wells and Bryce, 1993, fig. 96; Colin and Arneson, 1995:189, fig. 888; Gosliner, Behrens and Williams, 1996:170, fig. 601), *N. purpureolineata* O'Donoghue, 1924 (Wells and Bryce, 1993, fig. 91), *N. rutilans* (Pruvot-Fol, 1931) (Kent, 1893, pl. 13, fig. 9; Coleman, 1989:10; Wells and Bryce, 1993, fig. 97) and *N. megalocera* Yonow, 1990. Three of these species have an asymmetrical arrangement of denticles on the rachidian teeth. The radula is unknown in *Nembrotha rutilans*. In addition to the species listed by Cervera et al., *Nembrotha tabescens* (Risbec, 1928) also appears to be closely related to these species and has a similar color pattern (Risbec, 1928, pl. 5, fig. 9, as *Polycera tabescens*; Coleman, 1989:11). Of these species, all but *N. megalocera* have reddish rhinophores. Those of *N. megalocera* are black. All five of these species have reddish gills, as in *N. chamberlaini*. However, *N. chamberlaini* is unique in having the rhinophores and gills with a uniform red pigment throughout. The remaining species have purplish, white and yellow pigment on the gill bases. Cervera et al. (1996) stated that specimens depicted by Baba (1976) and Gosliner (1987), as *N. purpureolineata*, probably represent one or more undescribed species. We concur with this view. These species will be treated in a subsequent paper.

The radula of all of the above species, where described, is similar in its formula, and shape and dentition of teeth. All of these species, with the exception of *N. tabescens*, have an asymmetrical rachidian tooth with a shallowly or deeply bifid cusp on the inner right side. In *N. tabescens*, the rectangular rachidian tooth was described as lacking denticles (Risbec, 1928). In *N. lineolata* and *N. megalocera* the rachidian tooth is broadest basally, while in *N. chamberlaini* and *N. pur-*

pureolineata it is broadest near the middle of the tooth.

Of the above mentioned species, the reproductive system has been described only for *N. megalocera* (Cervera et al., 1996). There are no significant differences in reproductive anatomy between this species and *N. chamberlaini*, although the number of rows of penial spines was not indicated for *N. megalocera*.

The consistent differences in color of the living animal of *N. chamberlaini* clearly distinguish it from other species of *Nembrotha* with a similar color pattern.

***Nembrotha milleri* sp. nov.**
(Figs. 7A; 8A, B; 9A-D)

TYPE MATERIAL. — Holotype: CASIZ 088086, 17 m depth, 200 m south of lighthouse, Dakak, Mindanao, Philippines, 1 April 1993, T. M. Gosliner. Paratypes: USNM 880178, one specimen, 13–19 m depth, s. side Pescador Island, off Cebu, Philippines, 7 May 1979, C. A. Child. CASIZ 096302, one specimen, 29 m depth, Black Forest, Balcasag Island, off Bohol, Philippines, 22 March 1994, G. C. Williams. CASIZ 085944, three specimens, one dissected, 12 m depth, Devil's Point, Maricaban Island, off Batangas, Luzon, Philippines, 23 March 1993, T. M. Gosliner. CASIZ 093968, one specimen, 7 m depth, Lehaga Island, off Manado, Sulawesi, Indonesia, 18 October 1993, Pauline Fiene-Severns. CASIZ 078579, one specimen, Bunaken Island, off Madando, Sulawesi, Indonesia, 19 May 1991, Pauline Fiene-Severns.

ETYMOLOGY. — *Nembrotha milleri* is named for Michael D. Miller, of San Diego, California. Mike is a good friend and webmaster extraordinaire, who first introduced us to the diversity of the Philippine opisthobranch fauna.

DISTRIBUTION. — Known from Luzon, Cebu and Mindanao, Philippines and Sulawesi, Indonesia.

NATURAL HISTORY. — *Nembrotha milleri* has not been found in association with specific prey. It has been observed crawling actively on reef and surfaces in 10–29 m depth.

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FIGURE 7. Living animals. A. *Nembrotha milleri* sp. nov. specimen from Batangas, Luzon, Philippines, photo by Mike Miller. B. *Nembrotha mullineri* sp. nov. specimen from Batangas, Luzon, Philippines, photo by Mike Miller. C. *Notodoris serенаe* sp. nov. specimen from Papua New Guinea, photo by T. M. Gosliner.



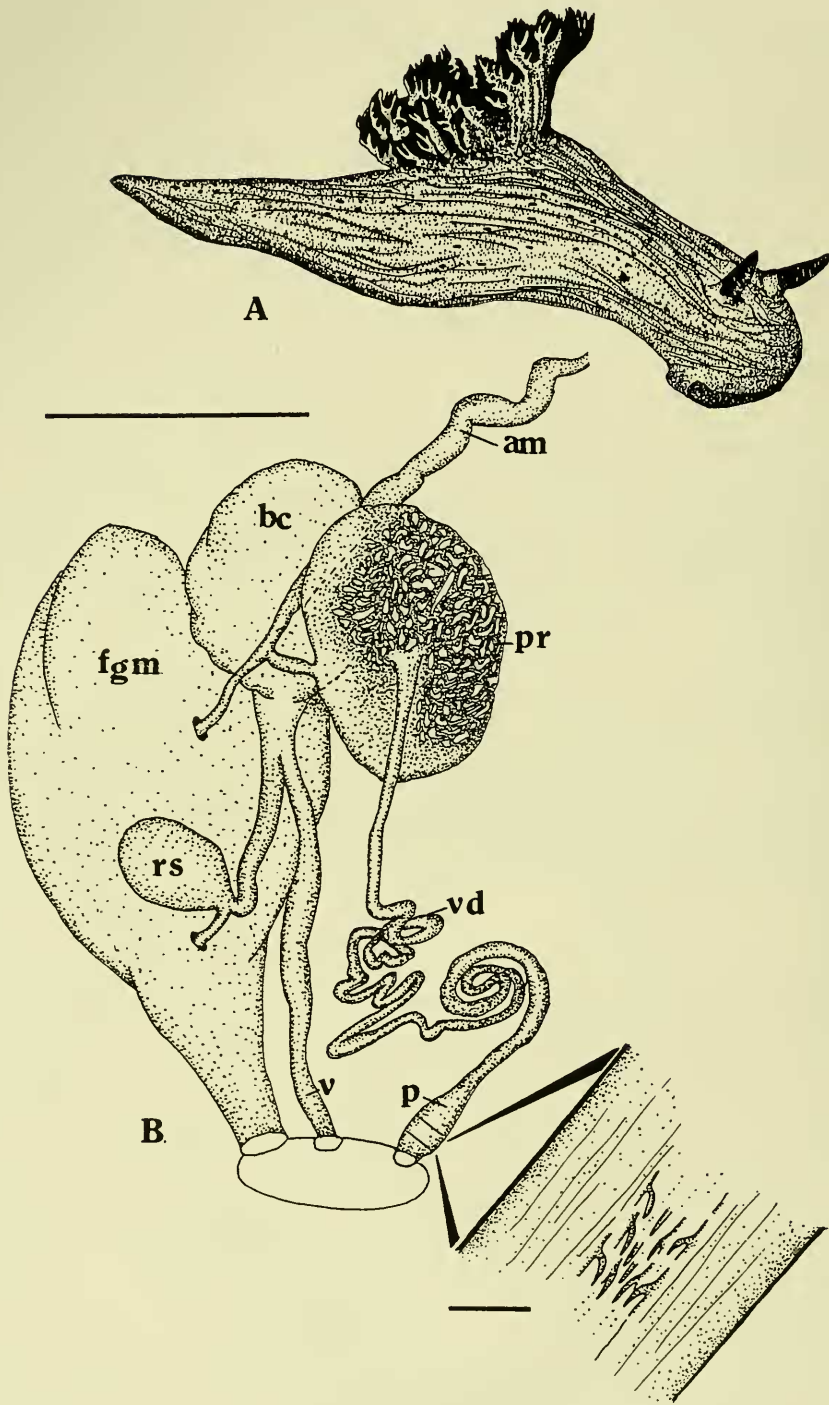


FIGURE 8. *Nembrotha milleri* sp. nov. A. Living animal. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 10 mm. Detail of penial armature, scale = 0.05 mm.

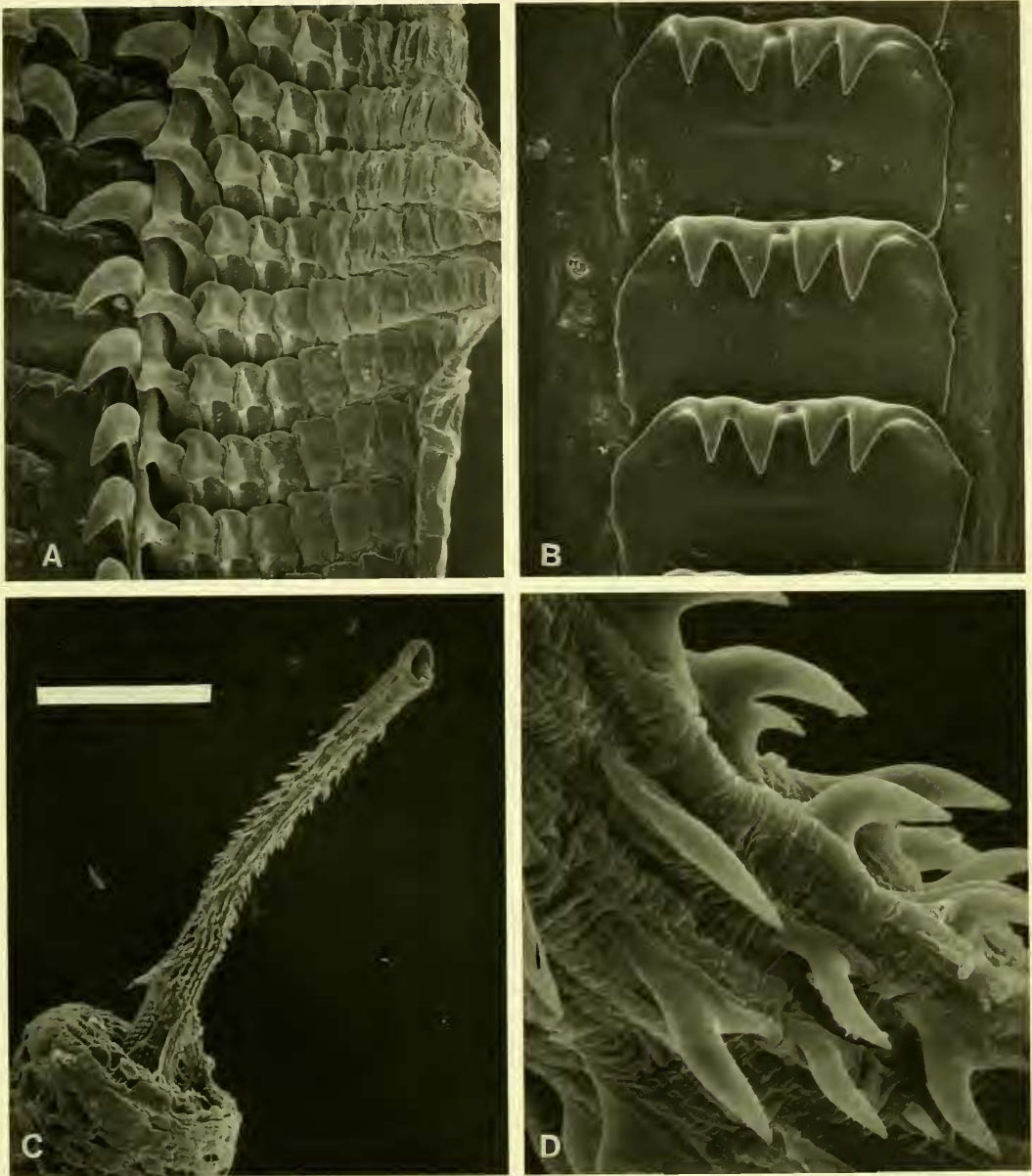


FIGURE 9. *Nembrotha milleri* sp. nov. Scanning electron micrographs. A. Half-row of radular teeth, scale = 430 μm . B. Rachidian teeth, scale = 200 μm . C. Protruded penis, scale = 200 μm . D. Penial armature, scale = 15 μm .

EXTERNAL MORPHOLOGY. — The body is elongate, limaciform and slightly undulate. The preserved animals are 30–60 mm in length. The living animals (Fig. 7A, 8A) are deep grey-green with longitudinal creases over the entire body surface. These creases extend up the gill stalks and are black in color. The tips of the five mul-

tipinnate gills, arising from three basal mounds, are black. The anus is a tall tube situated in the middle of the three gill bases. The rhinophores are perfoliate with 33 lamellae and arise from a smooth tapering sheath, similar in color to that of the body. The clavus is black. The genital aperture is situated midway between the rhinophores

and the anterior portion of the gills. There are two circular-shaped oral tentacles with a depression at the center of each. The body wall is highly muscularized.

BUCCAL ARMATURE. — The buccal mass is a large glandular oral tube anteriorly. The labial cuticle forms a brown chitinous disk, without distinct armature or rodlets. The radular formula of one specimen is $30 \times 8-10.1.1.1.8-10$ (Fig. 9A, B). The rachidian teeth (Fig. 9B) are broad and quadrangular with four symmetrically arranged triangular denticles. The inner laterals are much larger than the outer ones and have an elongate, curved terminal cusp and a shorter more basal one. The second, third and fourth laterals bear large cusps of decreasing size, while the remaining laterals are quadrangular without cusps (Fig. 9A).

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Figure 8B). The preampullary duct is short and narrow. It expands into an elongate, slightly convoluted ampulla which divides into an elongate oviduct and the vas deferens. From this point the oviduct enters the massive female gland mass. The short branch of the vas deferens widens into a huge, spherical prostatic portion, which has a dense network of interconnecting tubules over its surface. The vas deferens again narrows into an elongate, straight section followed by a highly convoluted ejaculatory segment that is muscularized. Within this muscular portion are a series of 14–24 crowded rows of curved, chitinous hooks (Fig. 9C, D). Basally there are up to 24 rows of spines which gradually diminish to 14 rows at the apex. The distal spines are slightly more elongate than the proximal ones. The short uterine duct emerges from the female gland mass and joins the saccate receptaculum seminis via a very short, curved duct, and continues proximally until it widens slightly, joining with the vagina. Together they enter the massive, thin-walled bursa copulatrix. In situ, the bursa is entirely surrounded by the prostate. In Fig. 8B, the prostate has been teased apart from the bursa and is shown positioned to the side. The elongate, wide vagina also emerges from the base of the bursa and shares a common base with the uterine duct. The vagina is separate from the vas deferens for its entire length.

DISCUSSION. — *Nembrotha milleri* and *N. mullineri* are both stockier, more robust species than other members of the genus. Three other

described species of *Nembrotha* have greenish pigment on the body. However, the primary body color of *N. kubaryana* Begh, 1877 and *N. cristata* Bergh, 1877 is black rather than green. In both of these species, the green pigment is found on large rounded tubercles, which are absent in *N. milleri*. The radular teeth of *N. cristata* are rounded rather than quadrangular and with five denticles rather than four. The penial armature of *N. cristata* and *N. mullineri* differs markedly from that of *N. milleri*. In these species, the basal spines are much larger than the distal ones, while in *N. milleri* the distal spines are slightly larger than the basal ones. *Nembrotha milleri* has far more rows of penial spines (up to 24) than do *N. cristata* (10–12) or *N. mullineri* (16–18). It appears that the distribution and size of penial spines can be used to differentiate species of *Nembrotha*. However, at present this feature has not been described for the majority of members of the genus.

Nembrotha milleri can be distinguished by its shiny, satin, gray-green body color.

***Nembrotha mullineri* sp. nov.**
(Figs. 7B; 10A, B; 11A-D)

TYPE MATERIAL. — Holotype: CASIZ 085941, 23 m depth, Layaglayag Point, Maricaban Island, Batangas, Luzon, Philippines, 22 March 1993, Kay Lieb. Paratypes: CASIZ 106507, one specimen, dissected, 8 m depth, Layaglayag Point, Maricaban Island, Batangas, Luzon, Philippines, 16 April, 1996, T. M. Gosliner. CASIZ 106508, two specimens, 12 m depth, Sepok Point, Maricaban Island, Batangas, Luzon, Philippines, 16 April 1996, M. Miller and J. Allen. CASIZ 103724, one specimen, 10 m depth, Hamilo, Batangas Province, Luzon, Philippines, 4 March 1995, T. M. Gosliner.

ETYMOLOGY. — *Nembrotha mullineri* is named for David K. Mulliner of San Diego, California, who first collected this species. Dave is an old friend and has contributed much to our knowledge of opisthobranch mollusks.

DISTRIBUTION. — Thus far, known only from Batangas Province, Luzon, Philippines.

NATURAL HISTORY. — *Nembrotha mullineri* is found crawling in the open on reef and rubble surfaces in 8–23 m depth. One specimen was observed on an unidentified arborescent bryozoan.

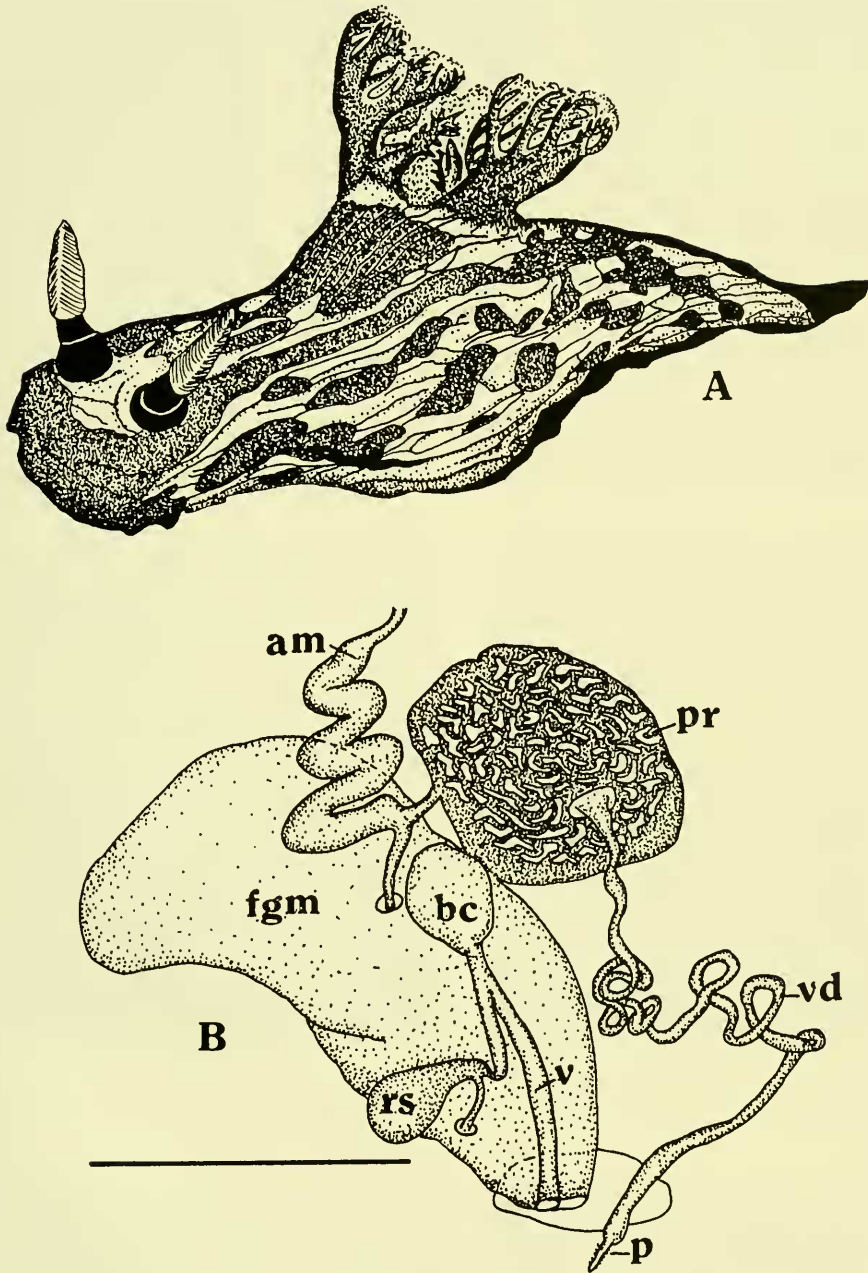


FIGURE 10. *Nembrotha mullineri* sp. nov. A. Living animal. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 10 mm.

EXTERNAL MORPHOLOGY. — The body is robust and limaciform. The preserved animals are 30–70 mm in length. The living animals (Fig. 7B, 10A) may exceed 100 mm in length. They

are creamy white, covered with a series of longitudinally oriented creases or wrinkles. There are large blotches and areas of brown over the entire body. The amount of brown blotching varies

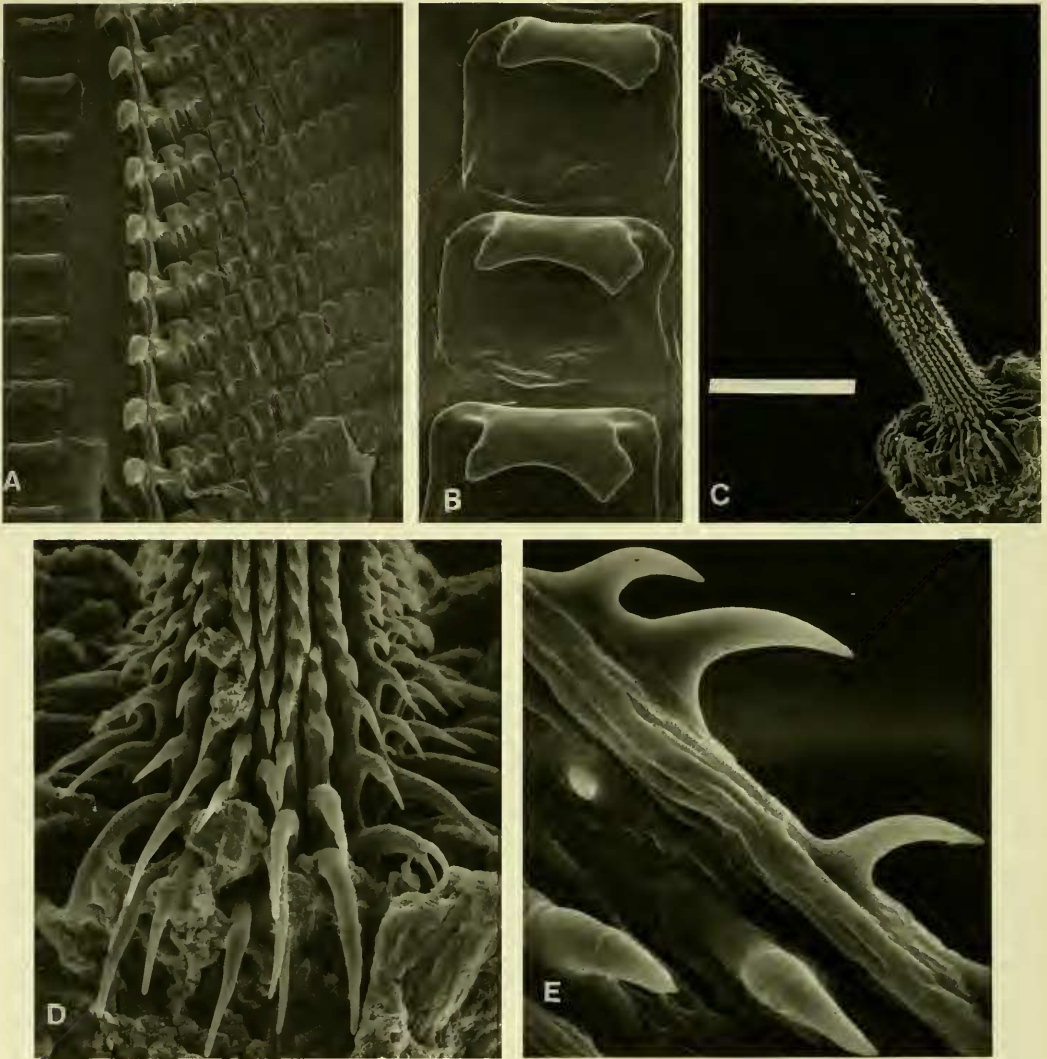


FIGURE 11. *Nembrotha mullineri* sp. nov. Scanning electron micrographs. A. Half-row of radular teeth, scale = 600 μm . B. Rachidian teeth, scale = 200 μm . C. Protruded penis, scale = 200 μm . D. Detail of basal penial spines, scale = 43 μm . E. Detail of distal penial spines, scale = 15 μm .

considerably in different individuals. It may be limited to a series of spots, elongate lines or form dense patches of brown. There are a few scattered, low, pointed tubercles situated between the creases in the brown areas. They are a greyish brown in color with dark brown tips. The head is rounded and dark brown in color. The rhinophores and outside of the five multipinnate gills are dark brown. The inner side of the gill base is cream and brown pigment is situated on the gill rachis and pinnae. The two posterior gills on each

side have a common base. The anus is situated between the gills on an elongate papillae. The genital aperture is located on the right side of the body, midway between the rhinophores and the anterior end of the branchial plume. The oral tentacles are short, blunt folds.

BUCCAL ARMATURE. — The buccal mass is large and muscular. The labial cuticle is devoid of rodlets or other armature. The radular formula in one specimen is $26 \times 11.1.1.1.11$ (Fig. 11 A, B). The rachidian teeth (Fig. 11B) are broad and

quadrangular. The masticatory margin has two triangular denticles that are joined by a curved marginal arch. The inner lateral teeth are elongate with a short, curved apical cusp and a short secondary cusp near the base of the tooth. The second, third and fourth laterals have a short cusp on their inner side, while the remaining teeth entirely lack a cusp and are quadrangular in shape decreasing in size towards the outer radular margin.

REPRODUCTIVE SYSTEM. — The reproductive system (Fig 10B) is triaulic. The preampullary duct is short and narrow. It expands into an elongate, highly convoluted ampulla which divides into an elongate oviduct and the vas deferens. From this point the oviduct enters the massive female gland mass. The short branch of the vas deferens widens into a huge, spherical prostatic portion which has a dense network of interconnecting tubules over its surface. The vas deferens again narrows into an elongate, highly convoluted ejaculatory segment that is muscularized. Within the distal end of this muscular portion are a series of 10–18 crowded rows of curved, chitinous hooks (Fig. 10C, D). Basally, there are up to 18 rows of spines which gradually diminish to 10 rows at the apex. The spines are of three different sizes and shapes (Fig. 11C). The basal spines (Fig. 11D) are elongate and curved, more than five times the length of the spines immediately distal to them. These short spines are short and curved. The distal two-thirds of the penis is armed with medium-sized spines that are about twice the length of the shortest ones (Fig. 11E), a few of which are bifid. The short uterine duct emerges from the female gland mass and joins the saccate receptaculum seminis via a short, curved duct, and continues proximally until it widens slightly and enters the spherical, thin-walled bursa copulatrix. In situ, the bursa is entirely surrounded by the prostate. In Fig. 11B, the prostate has been teased apart from the bursa and is shown positioned to the side. The elongate, wide vagina also emerges from the base of the bursa and shares a common base with the uterine duct. The vagina is separate from the vas deferens for its entire length.

DISCUSSION. — *Nembrotha mullineri* is most similar to *N. milleri* in its body form and shape. *Nembrotha mullineri* is the only member of the genus that is cream colored with brown spots or blotches. It has some scattered tubercles, but they

are less prominent than in species such as *N. guttata* (Yonow, 1993, fig. 6e), *N. cristata*, *N. kubaryana* and *N. nigerrima*. These four other tuberculate species have a black body color with green or orange pigment on the tubercles.

The rachidian tooth of *N. mullineri* is unique among described members of the genus in having an arched masticatory margin without distinctly separated denticles. The reproductive system of *N. mullineri* is similar to that described for *N. milleri*, except that the portion of the ejaculatory duct near the prostate is more highly convoluted. The penial morphology of *N. mullineri* is similar to that described for *N. cristata* (Bergh, 1905, pl. 18, figs. 7-8) where the basal penial spines are markedly longer than those immediately distal to them. This is in contrast to *N. milleri*, where there are only small basal spines.

Family NOTODORIDIDAE Bergh, 1875

Notodoris Bergh, 1875

Notodoris serенаe sp. nov. (Figs. 7C; 12A, B; 13A-D)

Notodoris sp. Allen and Steene, 1994:195; Colin and Arneson, 1995:190, fig. 896; Gosliner, Behrens and Williams, 1996:172, fig. 610.

TYPE MATERIAL. — Holotype: CASIZ 107228, RVS 143, Belau, 6 October 1987, R. Van Syoc. Paratypes: CASIZ 107230, two specimens, 12 m depth, barrier reef wall, Madang Lagoon, Madang, Papua New Guinea, 13, 14 August 1989, T. M. Gosliner. CASIZ 076318, one specimen, 25-30 m depth, Cauayan Rock, N. Palawan Island, Philippines, 9 March 1984, A. J. Ferreira. CASIZ 107232, one specimen, dissected, RVS 138, Belau, 4 October 1987, R. Van Syoc. CASIZ 107229, four specimens, two dissected, Madang Lagoon, Madang, Papua New Guinea, August 1989, T. M. Gosliner. CASIZ 107231, 10 m depth, Wongat Island dropoff, 29 July 1989, S. Jebb. CASIZ 086690, one specimen, 15 m depth, Unjuran reef, Flores, Indonesia, 29 April 1992, P. Fiene-Severns. CASIZ 073087, one specimen, Rasch Passage, Madang Lagoon, Madang, Papua New Guinea, 25 October 1986, G. Williamson.

ETYMOLOGY. — *Notodoris serенаe* is named for Serena Jebb who found some of the first specimens of this species and is an enthusiastic supporter of this research.

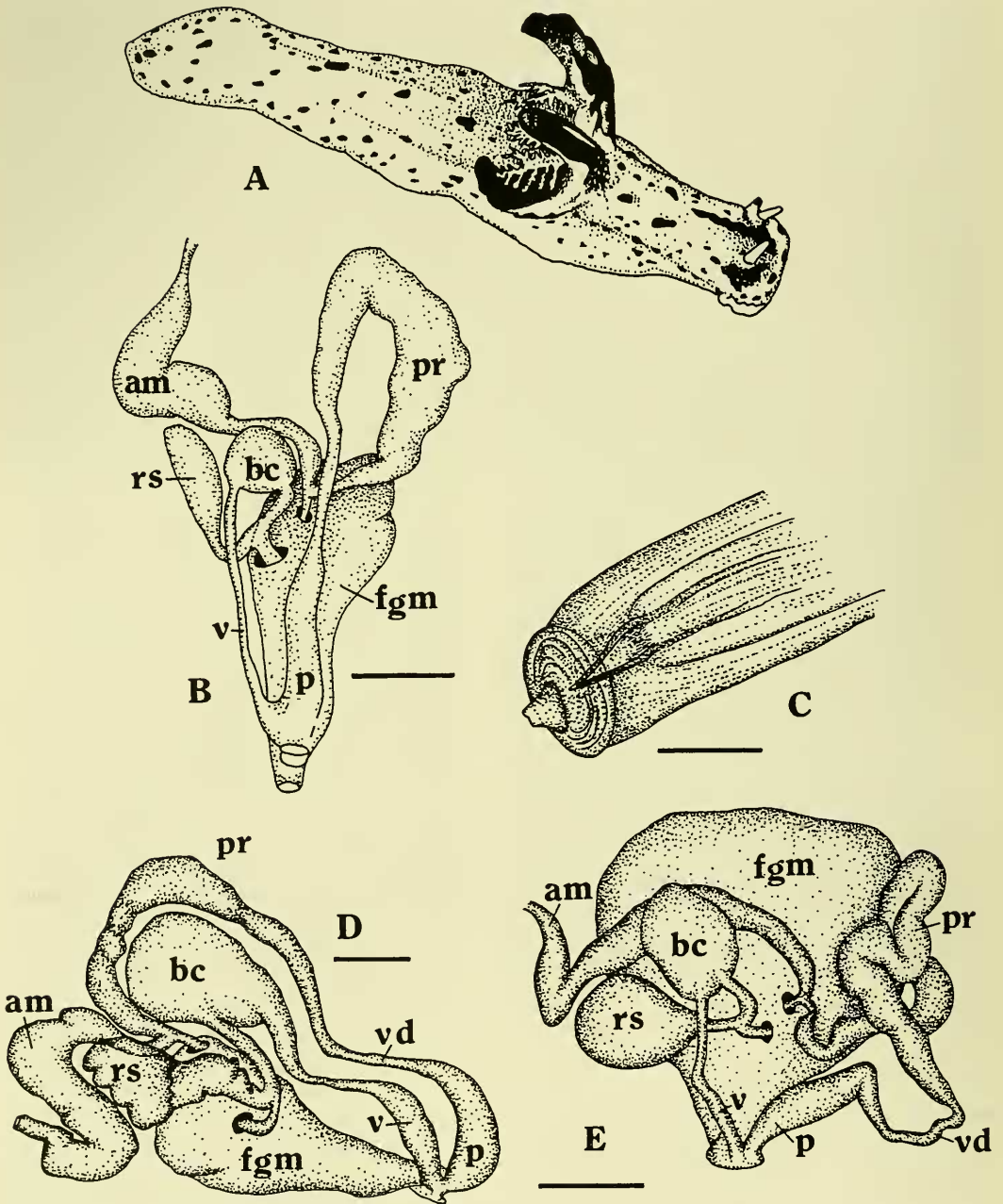


FIGURE 12. A. *Notodoris serenae* sp. nov., living animal. B. *Notodoris serenae* sp. nov., reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, scale = 1.0 mm. C. *Notodoris serenae* sp. nov., detail of penial papilla, scale = 0.25 mm. D. *Notodoris minor* Eliot, 1904, reproductive system, lettering as in A, scale = 1.0 mm. E. *Notodoris gardineri* Eliot, 1908, reproductive system, lettering as in A, scale = 1.0 mm.

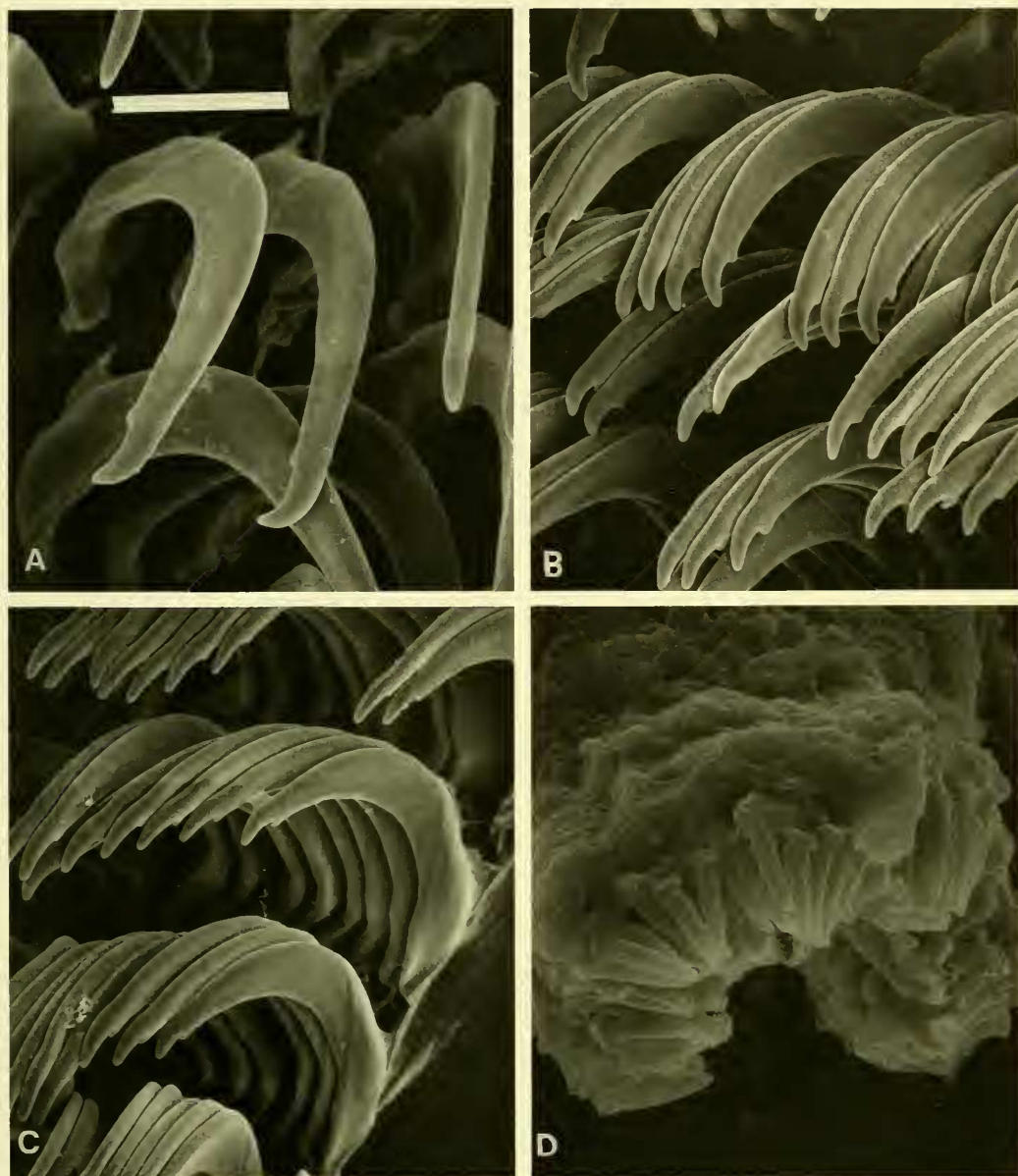


FIGURE 13. *Notodoris serenae* sp. nov. Scanning electron micrographs. A. Inner lateral teeth, scale = 43 μm . B. Middle lateral teeth, scale = 75 μm . C. Outer lateral teeth, scale = 75 μm . D. Penial armature, scale = 10 μm .

DISTRIBUTION. — Thus far this species is known from Papua New Guinea, Indonesia, Malaysia, Philippines, Belau, Pohnpei and Okinawa (C. Carlson, present study and P. J. Hoff, pers. comm.).

NATURAL HISTORY. — *Notodoris serenae* is found in 10–15 m depths on the edges of the crest

of barrier reefs. It feeds upon the calcareous sponge *Leucetta chagosensis* Dendy, 1913 (present study), not *L. primigenia* Haeckel, 1872, as erroneously indicated in Gosliner, Behrens and Williams (1996:172).

EXTERNAL MORPHOLOGY. — As in other species of *Notodoris*, *N. serenae* is firm bodied and

limaciform. The preserved animals examined were up to 58 mm in length. The living animals, which reach 100 mm in length (Fig. 7C, 12A), are dull white to grey with randomly distributed and variably sized low black tubercles and markings. The foot is yellow throughout and its margin is visible dorsally and laterally when the animal is crawling. The gills are yellow or green with black tips. There are three large, firm, arching appendages surrounding the gills, the medial of which is shorter than the two laterals. A pattern of reticulating ridges adorn each appendage. The ridges are marked with black, becoming densest at their tips. The head is angular, accentuated by a series of ridges of irregular black-tipped tubercles. The rhinophores are simple, smooth and bright yellow. The head bears a raised medial ridge, which is black. It begins anterior to the rhinophores and continues posteriorly. It may continue as a broken series of tubercles. A series of irregular tubercles, each black-tipped, are situated laterally to each rhinophore. There is a separation between the head and foot forming a groove and two oral lappets on either side of the head. The genital aperture is situated on the right side of the body, immediately posteroventral to the rhinophores.

BUCCAL ARMATURE. — There is a thin chitinous labial cuticle devoid of rodlets or armature. Salivary glands are thin and strap-like. The radular formula in two specimens is $32 \times 30-32.030-32$. The teeth from the inner portion of the radula (Fig. 13A), middle (Fig. 13B) and outer margin (Fig. 13C) are all evenly arched and hamate, with a single rounded denticle situated just below the primary cusp.

REPRODUCTIVE SYSTEM. — The arrangement of organs is triaulic (Fig. 12B). The preampullary duct is short and straight. It widens into the thick, curved ampulla, which again narrows and bifurcates. The short oviduct enters the female gland mass, which was not fully mature in the single large individual examined. The vas deferens expands into a thick, curved prostatic portion which narrows into a short, straight ejaculatory portion. This segment again widens into the penial sac. The tip of the penis bears a small cuticular tube that protrudes from the apex. Immediately proximal to the apex is an area of darkly staining cells (Fig. 12C) which contains minute penial spines visible under the light microscope at $1000 \times$ magnification. Scanning electron micrographs

confirm the presence of these minute penial spines (Fig. 13D). The uterine duct emerges from the female gland mass and widens and joins the elongate duct of the pyriform receptaculum seminis. Together these ducts enter the posterior end of the small, spherical bursa copulatrix. From the other end of the bursa, the thin, straight vaginal duct connects with the penial sac just proximally of the genital aperture.

DISCUSSION. — The predominantly gray body color of *N. serenae* differs significantly from the common bright yellow color found in three other described members of this genus: *Notodoris gardineri* Eliot, 1908, *N. minor*, Eliot, 1904 and *N. citrina* Bergh, 1875. The presence of three elongate extrabranchial appendages and three multipinnate gills are also unique to *N. serenae*. The remaining species have three branchial lappets that overhang and protect the gills. In *N. minor* these lappets are simply rounded while in *N. gardineri* and *N. citrina* their margin is distinctly lobed. The lobes are deeper in *N. gardineri* than in *N. citrina*. These three species have arrangements of gills that differ markedly from those of *N. serenae*. In *N. gardineri* and *N. minor*, there are numerous small gills, while in *N. citrina*, there are seven quadripinnate gills (O'Donoghue, 1924).

The radular teeth of *Notodoris serenae* are more deeply bifid as in *N. gardineri* (O'Donoghue, 1924, figs. 63-64; Thompson, 1975, fig. 4; Yonow, 1993, fig. 8a, b) rather than having the more shallow lobes found in *N. minor* (Eliot, 1904, pl. 3, fig. 1g) and *N. citrina* (Bergh, 1875, pl. 9, 10). The radula of *N. citrina* is much narrower than that of the other species. Bergh (1875) indicated that there were only 14 teeth per half-row in *N. citrina* while in the other species there are 25-42 teeth per half-row.

The reproductive system has not been fully described for any other species of *Notodoris*. Thompson (1975) indicated that the penis of *N. gardineri* has small spines, but did not illustrate this feature. The arrangement of the bursa copulatrix and receptaculum seminis of *N. citrina* was illustrated by Bergh (1875). To compare the reproductive anatomy of *N. serenae* to other members of the genus, specimens of *N. minor* (CASIZ 068668) and *N. gardineri* (CASIZ 068693) from Papua New Guinea were dissected (Fig. 12 D and E, respectively). The general arrangement of organs is similar in all three species examined. In

all cases, after merging with the duct of the receptaculum seminis, the uterine duct enters the wall of the bursa copulatrix rather than the base of the bursa. This configuration was also described for *N. citrina* (Bergh, 1875). In *N. gardineri*, there is a faint area near the subapical portion of the penis, which may bear spines. In *N. minor*, the penis is slightly more protruded and the penial spines are obvious, but minute. The penial spines found in the specimens of *N. serенаe* examined here are larger than those of *N. gardineri*, but smaller than those of *N. minor*.

Thompson (1975) in his discussion of *N. gardineri*, stated that *N. citrina* and *N. minor* had not been found since their original descriptions and doubted the validity of three distinct species of *Notodoris*. Reexamination of additional material of these species and *N. serенаe*, confirms the distinctness of four species of *Notodoris*. The characteristics employed by O'Donoghue (1924) to separate the species are indeed valid. Additionally, characteristics of the branchial lappets clearly distinguish the species, as do consistent differences in color pattern.

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